DIOECISM IN CITHAREXYLUM (VERBENACEAE)

P. B. TOMLINSON AND PRISCILLA FAWCETT

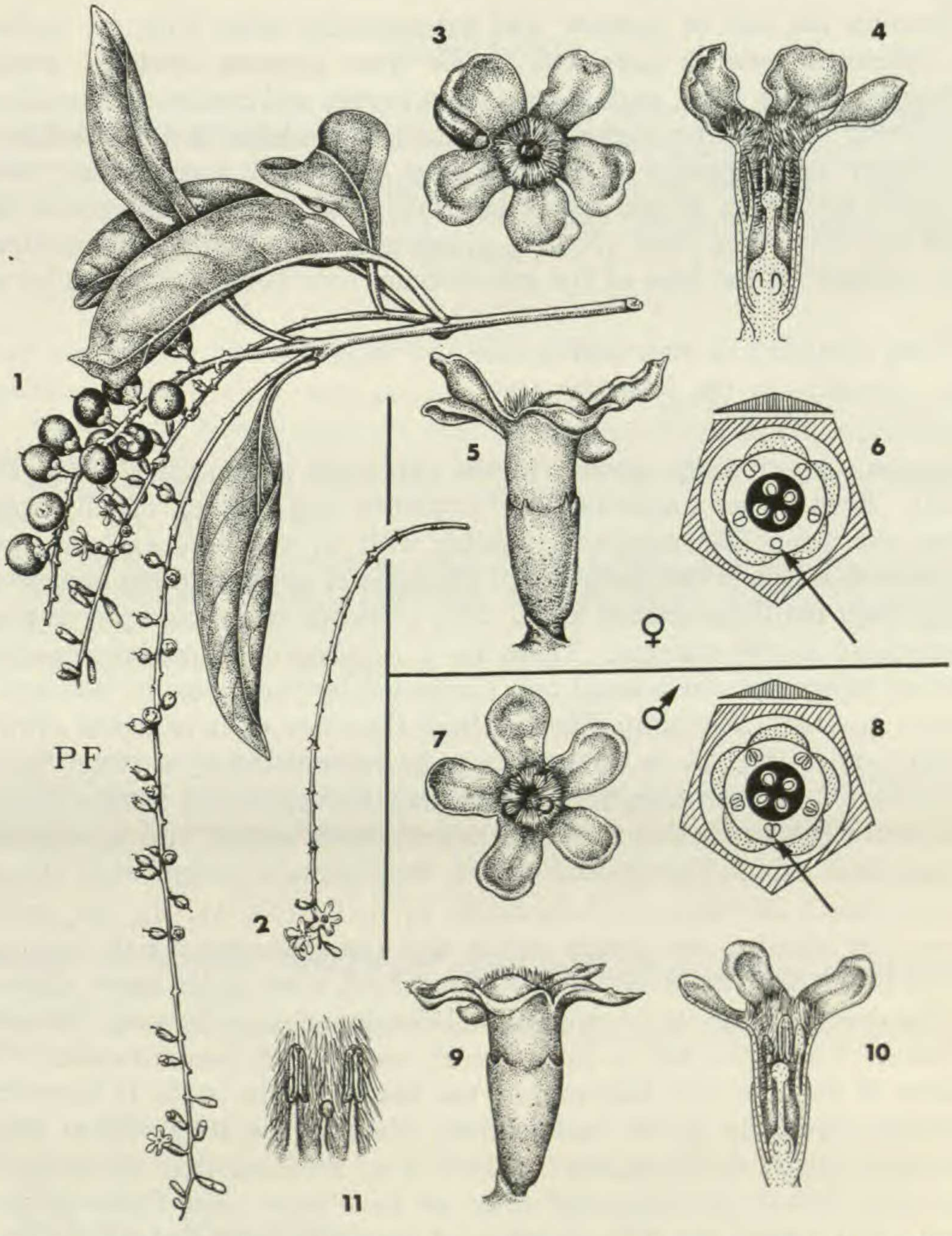
OUTBREEDING MECHANISMS ARE A feature of perennial plants (Stebbins, 1950 p. 165 *et seq.*) and their high incidence in trees is well known. This high incidence is related to the evolutionary advantages of outcrossing in terms of genetic flexibility. In continuing studies of the distinctive woody flora of South Florida it is evident that the majority of species have some simple and obvious mechanism for outcrossing such as dioecism, self-incompatibility as suggested by heterostyly, and other kinds of morphological polymorphism. Field study is revealing further examples among species which have hitherto been thought to have perfect flowers.

The present article refers to such an example in *Citharexylum fruticosum* L. ("Fiddlewood"). *Citharexylum* L. is a genus of some 100 species in Central and South America. The flowers seem largely to have been described as "perfect" (e.g. Sargent, 1894). *Citharexylum fruticosum* itself is widely distributed in the Caribbean area and a number of varieties have been described (Moldenke, 1959). In South Florida it is scattered in pinelands and hammocks on the Florida Keys and northward with a limited coastal distribution. The species tends to be a pioneer in recently burnt pineland and persists in more or less closed hammock communities which are the climax communities in many fire-free areas. The species shows distinct weedy tendencies and is not uncommon on disturbed sites. From this ease of spread and existence in natural communities it is an evident member of the native flora.

Descriptions of this tree in floras and other manuals dealing with this part of the United States (e.g. Chapman (1897), Sargent (1894), Small (1933), West and Arnold (1946)) or those which refer to it in other parts of its range (e.g. Britton and Millspaugh (1920), Léon and Alain (1957), Little and Wadsworth (1964), Moldenke (1954)) suggest, directly or indirectly, that flowers are perfect. In South Florida, at least, it is dioecious. This observation has been overlooked because the flowers in the two sexes are very similar and casual examination of herbarium specimens would not reveal the constant differences shown in field populations.

OBSERVATIONS

Phenology and Sexuality. *Citharexylum* begins to flower in early summer in South Florida (May–June). The flowers are on slender pendulous spikes which are either terminal on or from the upper leaf axils of current-year shoots (FIGURE 1). During the summer months several generations of renewal shoots with flowering branches may be produced so that the flowering period is extended. Flowers, however, do not occur



FIGURES 1–11. **Citharexylum fruticosum** L., reproductive morphology, from specimens growing at the Montgomery Foundation, 11935 Old Cutler Road, Miami, Florida 33156. 1, female flowering shoot; 2, male spike; 3–6, female flower; 3, from above, 4, in longitudinal section, 5, from the side, 6, floral diagram; 7–10, male flower; 7, from above, 8, floral diagram, 9, from the side, 10, in longitudinal section; 11, detail of abaxial staminode and two adjacent stamens in a male flower. Figs. 1 & 2, × 1/2; figs. 3–5 & 7, 9 & 10, × 3; fig. 11, × 5.

"throughout the year" as has been stated in several publications, all of which seem to have their origin in the description by Sargent (1894). The phenology and general growth pattern of this tree is very distinctive and requires detailed study, a statement which could be repeated for all the woody plants of South Florida.

Towards the end of summer, and subsequently when fruit set begins, the difference between male and female trees becomes obvious. Fruits enlarge on female trees; male trees remain barren and can be distinguished throughout the fruiting season (September–December) by the pendulous but empty inflorescences. This distinction is evident even earlier, since fertilized flowers on female spikes lose only their corollas but retain the calyx and developing pistil (FIGURE 1, below). Male flowers fall as a unit after anthesis so the base of the inflorescence axis becomes bare (FIGURE 2).

Trees identified as male and female and tagged in one year retain their same sexuality in the following year.

Flowers. Superficially, flowers in the two sexes are identical (FIGURES 3–10). Each flower has a tubular, 5-toothed calyx which usually splits down one side. The corolla is tubular with 5(–6) more or less equal petal-lobes although the members of the adaxial pair are often somewhat larger than the three abaxial lobes. This tendency to zygomorphy is most pronounced in the stamens. There are 5 stamens or staminodes in each kind of flower but the adaxial one (indicated by the arrow in FIGURES 6 and 8) is usually distinctly different from the other 4; it is almost always smaller and it may be so reduced as to be represented by a mere vestige (FIGURE 11). In the male flower the 4 abaxial stamens are always fertile; dehiscence is introrse and the large pollen grains adhere into a relatively conspicuous mass. The adaxial stamen may contain pollen, even though it is reduced, but often it is vestigial, as in FIGURE 11. In the female flower the stamens are always sterile and the microsporangial tissue remains brown and never produces pollen. Such staminodes never dehisce.

The ovary appears to be equally well developed in both sexes (FIGURES 4 and 6; 8 and 10) with 4 equal ovules, one in each pseudoloculus. The stigma is more or less bilobed but the length of the style is somewhat variable, especially in the male flower. Usually the stigma is at about the same height as the stamens. There is no evidence that the ovules in the male flowers are functional since we have never seen fruits on male trees. The reason for this abortion of seemingly well-formed ovules is worthy of more detailed investigation.

Pollination. Flowers are sweet-scented during the day and nectar is secreted at the base of the ovary tube. Since the pollen is sticky it is evident that the flowers are insect pollinated but we have made no observations on the kinds of insect visitors. The mouth of the corolla tube is more or less occluded by a dense outgrowth of uniseriate multicellular hairs (FIGURES 3 and 7) and an insect probing for nectar would certainly touch both stigma and pollen mass. Self-fertilization of male flowers would seem to be quite easy.

Fruit set on female trees is very abundant but there seems to be a high incidence of fruits with aborted embryos.

CONCLUSION

It seems evident from these morphological observations that *Citharexylum fruticosum* is dioecious and it may seem remarkable that such a simple observation could have escaped the attention of botanists. However, this is a general reflection on how poorly the tree flora of South Florida has been investigated by field workers.

LITERATURE CITED

BRITTON, N. L., & C. F. MILLSPAUGH. 1920. The Bahama Flora. Published by the authors. New York.

CHAPMAN, A. W. 1897. Flora of the southern United States. Ed. 3. Cambridge Botanical Supply Co., Cambridge, Massachusetts.

LÉON, H., & H. ALAIN. 1957. Flora de Cuba. Vol. 4. P. Fernandez, Havana.

LITTLE, E., & F. H. WADSWORTH. 1964. Common trees of Puerto Rico and the Virgin Islands. U.S.D.A. Handbook No. 249. Forest Service, Washington, D.C.

MOLDENKE, H. N. 1954. Verbenaceae in: Flora of Trinidad and Tobago. vol. II, pt. VI. Government Printing Office, Trinidad.

———. 1959. A résumé of the Verbenaceae, Avicenniaceae, Stilbaceae, Symphoremaceae and Eriocaulaceae of the world as to valid taxa, geographical distribution and synonymy. Published privately.

SARGENT, C. S. 1894. *Citharexylon* in: The Silva of North America. vol. VI. 101–103. *Pl. CCXCV*. Houghton Mifflin & Co. Boston & New York.

SMALL, J. K. 1933. Manual of the southeastern Flora. Published by the author. New York.

STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia University Press. New York.

WEST, E., & L. E. ARNOLD. 1946. The native trees of Florida. University of Florida Press. Gainesville.

(P. B. T.)
HARVARD UNIVERSITY
HARVARD FOREST
PETERSHAM, MASS. 01366

(P. F.)
FAIRCHILD TROPICAL GARDEN
10901 OLD CUTLER ROAD
MIAMI, FLORIDA 33156